Metamorphosis of the "Non-aquatic Frog" of the Palau Islands, Western Carolines

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INTRODUCTION

THE FROGS in the Palau Islands seldom, if ever, leave their refuges during the daytime, but after sunset they are found easily in weedy places. There are two types of frogs, the large and the small, of which the larger is the female and the smaller the male. The male has strong jumping powers. Neither type has any webs between toes or fingers.

The adult frogs are well known to the Palau natives, who call them "gedegedug," "hedehedh," or "dechedech," but it is interesting to know that no one has seen their tadpoles. I made a search for the tadpoles in some pools and ponds, but without success, and the question soon arose as to where and how these frogs pass through their larval stages. During my long stay in the Palau Tropical Biological Station on Koror Island, I was fortunate several times in discovering the spawning place of the frogs, and was thus given the opportunity to study their metamorphosis.

Here I wish to express my thanks to Professor Shinkishi Hatai, then Director of the Palau Tropical Biological Station, for his kind guidance throughout the observations.

METAMORPHOSIS

The eggs collected from the natural spawning place were placed in a petri dish, the bottom of which was covered with a wet filter paper to maintain a humidity of about 100 per cent. The room temperature ranged from 25.1° to 31.0° C. throughout the period of observation.

The observations were made on one hatch, of which the youngest larva is shown in Figure 1*a*. The egg is covered with a rather tough gelatinous membrane and just after spawning it measures about 6 mm. in diameter. A large mass of yellowish-white yolk is attached to the abdomen of the larva. The three parts of the body—head, trunk, and tail—are distinguishable. The central part of the head is somewhat hollow, and rudimentary eyes appear on both sides. The mouth is a shallow invagination not yet open. The end of the tail is bent toward the abdomen. Each pair of limbs appears as rounded and protuberant swellings, the hind limbs being slightly larger than the forelimbs. Fine blood vessels run along the forelimbs, then toward the abdomen and finally branch into networks. The melanophores are not yet visible.

On the second day (Fig. 1*b*), a pair of well-developed eyes appears and the mouth opens, the tail becomes much longer, and the vascular system is conspicuously developed. The melanophores appear scattered over the head and trunk.

On the fourth day (Fig. 1*c*), the mouth is wide open and a pair of external nares is seen on its upper part. Numerous blood vessels are distributed over the abdominal region; the heart, which is perceptible through the skin, beats at an average rate of 120 times per minute (at a temperature of 30.8° C.).

On the seventh day (Fig. 1*d, e*), the yolk decreases and becomes flattened dorsoventrally. Five toes can be distinguished in the hind limbs but the forelimbs are hidden by the yolk mass. The melanophores increase in number on both the head and trunk.

On the tenth day (Figs. 1*f*; 2*a*), both the

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hind limbs and tail become more developed, and the latter reaches about 4 mm. in length. The body length, except for the tail, is about 5 mm.

On the fourteenth day (Fig. 2*b*), the egg reaches about 9.5 mm. in diameter. The egg seems to expand day by day as the larva grows in it. The skin of the abdomen, which begins to expand from about the seventh day of development, swells conspicuously and forms a pair of large, balloon-like sacs with a great number of blood vessels on the walls.

On the seventeenth day (Fig. 2*c, d, e*), the greater part of both tail and yolk are absorbed, and, except for the extreme expansion of the abdominal skin, the larva closely resembles an adult frog.

On the nineteenth day (Fig. 2*f*), nearly all of the yolk has been consumed and the tail is now rudimentary. When the egg is carefully removed from the vessel, the gelatinous membrane readily slips off and a miniature frog jumps free.

After a few more days all the larvae complete their metamorphosis, and as soon as they leave their eggs, the expanded abdominal skin contracts to adhere closely to the abdomen, showing the same appearance as in the adult frog. These young frogs measure about 6 mm. in length from the tip of snout to the anus.

ADULT FROG

Some of the external features of the male and female frogs are shown in Figure 3*a–e*.

Both types of frogs are dark brown but the male is the darker. The inside of the thighs is yellowish-red. In some frogs a fine line arises from the tip of the rostral and extends over the ridge of the back to the toe.

The tip of the rostral is somewhat rounded and the outer nostrils open close to its extremity. The distance between the rostrum and the point where the upper and lower jaws unite is slightly longer than the rostrum region. The distance between the extremity of the rostrum to the joint of each jaw is approximately equal to the width of head. The pupil is ellipsoid. The circular tympanum is conspicuous. Its diameter is about one and a half times the length between the hind margin of the eye and the fore margin of the tympanum, and is slightly shorter than the distance between each outer nostril. Close to the upper margin of the tympanum there is a narrow skin fold.

In the buccal cavity a pair of internal nostrils, a pair of triangular vomerine tooth plates, and a tongue are found. The tip of the tongue is bifurcated. The two types of frogs have tongues of different shapes; that of the large (female) frog is slenderer than that of the small (male) frog, and the distance between each small process is less in the large frog than in the small frog. There are minute teeth in the upper jaw but not in the lower jaw. The vocal sac is not very evident.

Some skin folds are scattered over the dorsal part of the trunk. Of the fingers of the forelimb, the third is longest, then the first is next longest; the other two fingers are nearly equal in length. Of the toes of the hind limb, the fourth is much more prominent than the others, and the first is shortest. The webs are completely degenerated. Many rounded protuberances of skin are found on the insides of the fingers, toes, palm, and metatarsus. The tips of both fingers and toes are rounded. The length from the base of the tibia to the tip of the longest toe is two and a half times that from the base of the arm to the tip of the longest finger, and is 1.6 times the length from the tip of the rostrum to the anus.

DISCUSSION

The eggs upon which the observations were made were collected in the months of May, October, and December. They were

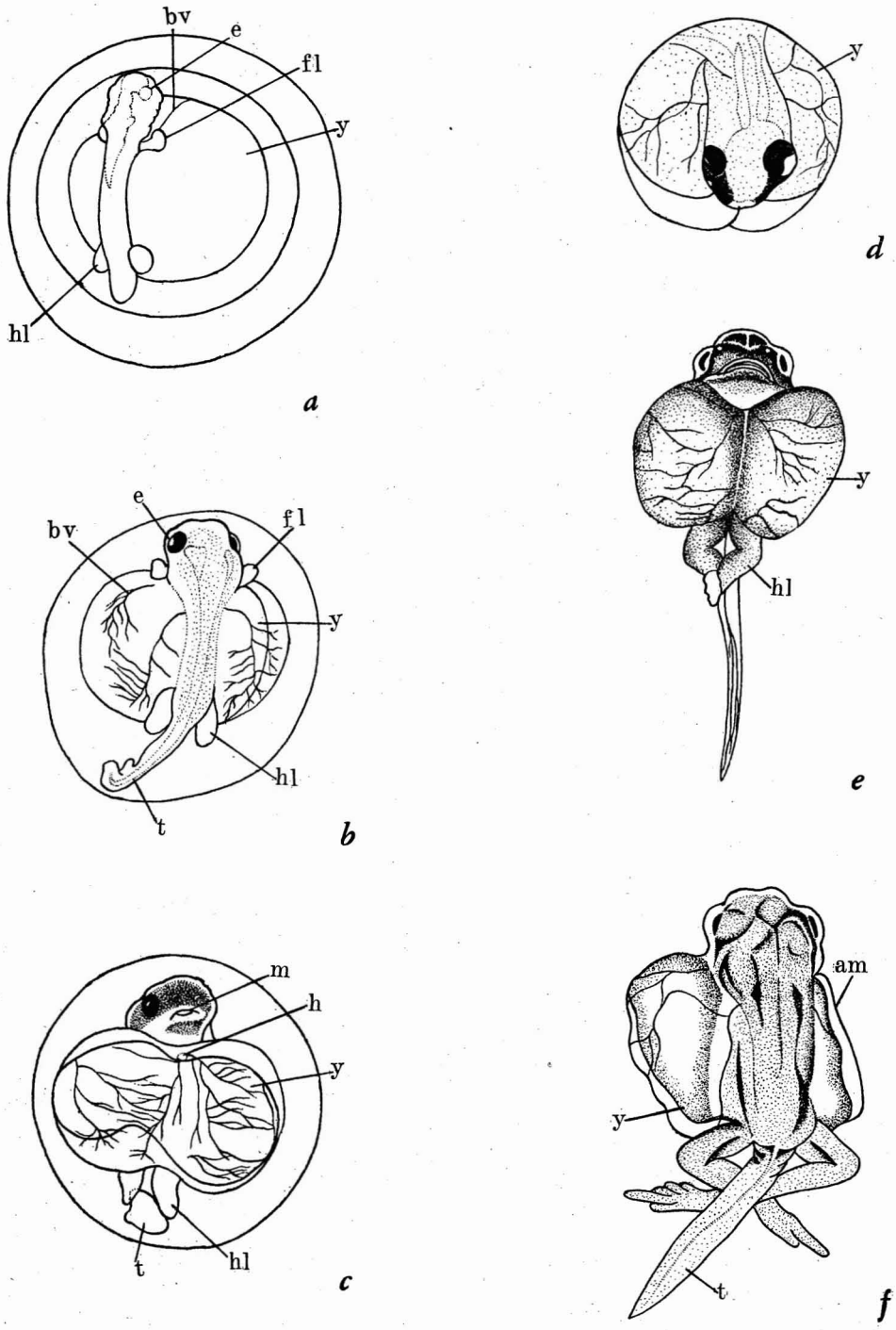

FIG. 1. Progressive stages of metamorphosis of the frog from the Palau Islands, × 7. *a,* Dorsal view of the youngest larva (the outer gelatinous egg membrane is omitted); *b,* 2 days later, dorsal view (only the innermost egg membrane is drawn); *c,* 4 days later, ventral view; *d,* 7 days later (all membranes are removed from the egg), frontal view; *e,* same as *d,* ventral view; *f,* 10 days later, dorsal view.

(am, Abdominal membrane; bv, blood vessel; e, eye; fl, forelimb; h, heart; hl, hind limb; m, mouth; t, tail.)

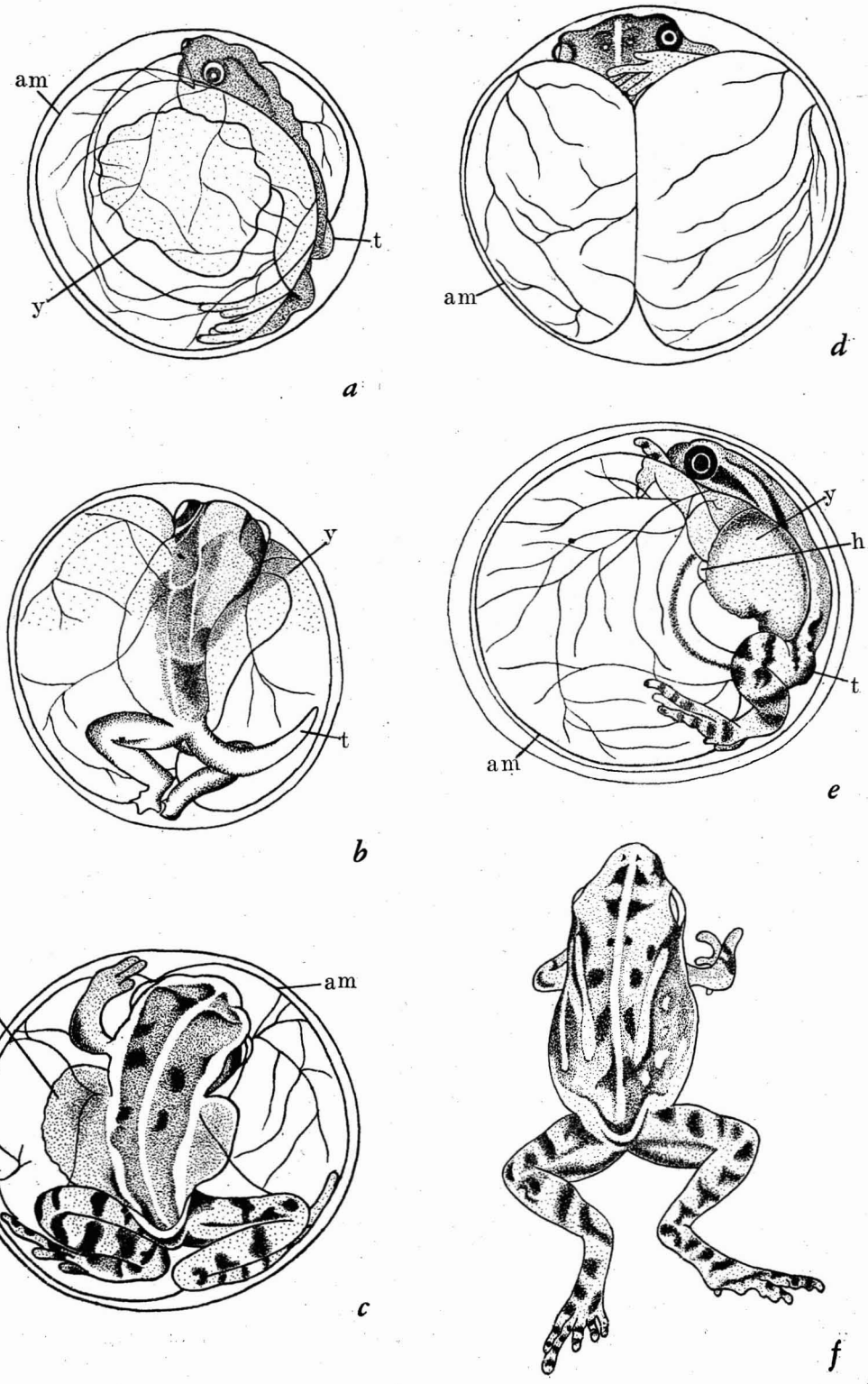

FIG. 2. Further stages in metamorphosis of the frog, × 7. *a,* Same as 1*f,* lateral view, only the innermost egg membrane is drawn; *b,* 14 days later, dorsal view; *c,* 17 days later, dorsal view; *d,* same as *c,* lateral view; *e,* same as *c,* ventral view; *f,* 19 days later, egg membranes removed, dorsal view.

spawned in a weedy place on the ground. The number of eggs in one hatch was usually about 30. At the time of each collection it was noticed that a considerable number of eggs with large yellow yolks could be seen through the skin in the abdomens of large frogs. These observations lead to the conclusion that the frogs have no definite spawning time, but spawn every month throughout the year.

Metamorphosis is completed so rapidly that the first stage observed was probably close to the earliest stage. Apparently, the time required to complete the metamorphosis is about 3 weeks.

The characteristic features of the metamorphosis of this frog are the extreme swelling of the abdominal skin and the absence of both external gills and gill clefts. The larva does not pass a free-swimming stage in water; therefore external gills for respiration are unnecessary. The larva grows rapidly within the egg, and metabolism takes place actively. The expansion of abdominal skin or the increase of body surface and the abundant blood vessels in the skin may be helpful in increasing respiration through the skin. In addition to these characteristics, the larva depends wholly upon the yolk for nutriment throughout metamorphosis, and its yolk is large, like that of a fish egg. Observations on the cleavage of the egg were not made.

Hitherto only two species of frogs have been known to exhibit behavior more or less similar to that of the Palau frog: *Hylodes* (= *Eleutherodactylus*) *martinicensis* (Peters 1876; Lynn 1940) and *Rana opisthodon* (Boulenger 1886). Both of them undergo their whole metamorphosis within their eggs, and their embryos possess neither gills nor gill openings.

Hylodes martinicensis lays its eggs on a broad leaf of a plant, and the eggs are then glued to the leaf. The egg measures 4–5 mm. in diameter. The metamorphosis is completed during 21 days, approximately the same time as was observed for the Palau frog. Its most noteworthy characteristic is the development of a large well-vascularized tail, the function of which is to serve as a respiratory organ, just as the extreme expansion of the abdominal skin of the Palau frog does for it.

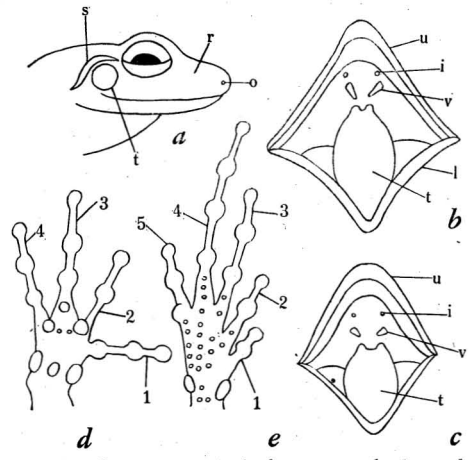

FIG. 3. Some external features of the adult frog. *a,* Lateral view of the head (approx. × 1.6; o, outer nostril; r, rostrum; s, skin fold; t, tympanum); *b,* buccal cavity of the large frog; *c,* same of the small frog (*b* and *c,* approx. × 2; i, internal nostril; l, lower jaw; t, tongue; v, vomerine tooth plate; u, upper jaw); *d,* palm and fingers (approx. × 2.6; 1, 2, etc., the first, second, etc., fingers); *e,* metatarsus and toes (approx. × 2.6; 1, 2, etc., the first, second, etc., toes).

Rana opisthodon deposits its eggs in moist crevices of rock close to water. Its egg measures 6–10 mm. in diameter. Its embryo develops without any evidence of a tail, and has as breathing organs several regular transverse folds on each side of the abdomen which function in a manner quite similar to *Hylodes'* tail. Thus the Palau frog is entirely different from these two species.

At present it seems that the data are not sufficient to determine the genus to which the Palau frog belongs. Although both hand and foot well resemble those of *Hylodes,* the other general features rather resemble those of the Ranidae, and the frog probably is a new species of *Rana.* The two types of frogs

found, the small and the large, seem to indicate the occurrence of sexual dimorphism in the species.

SUMMARY

1. The frog described in this article is commonly found in the Palau Islands. There are two types, large and small, apparently an effect of sexual dimorphism. Neither type possesses webs between toes or fingers. This frog is probably a new species of *Rana.*

2. The number of eggs in one hatch is about 30 and they are spawned on the ground in weedy or bushy places. Metamorphosis is completed in the egg, and the frogs do not experience the free-swimming stage of a tadpole. About 3 weeks are required for complete metamorphosis.

3. During metamorphosis neither external gills nor gill clefts appear, but the abdominal skin expands to an extreme degree.

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